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ORIGINAL ARTICLE

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From the inverse density–area relationship to the minimum patch size of a host–parasitoid system

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Abstract The minimum amount of suitable habitat (MASH) is an important concept in conservation biological control. Two methods for estimating the MASH have been proposed by McCoy and Mushinsky based on an inverse density–area relationship. Using data of the population densities of aphid host–parasitoid–hyperparasitoid collected from wheat fields of different habitat sizes, we argued that the inverse density–area relationship may be an artifact. Significant correlations between population densities and patch sizes from all three trophic levels were found once the population density had been log-transformed. We could not obtain the same results if the population density had not been log-transformed. We estimated that the MASH for the aphid *M. avena*, *S. graminum*, *A. avenae*, *A. gifuensis*, *P. aphidis*, and *Alloxysta* sp. were 246, 246, 479, 495, 949, and 835 m^2 according to the methods of McCoy and Mushinsky. The scale-dependence and the systematic spatial variations of the host–parasitoid interaction suggests that we can achieve an optimal effect of biological control by manipulating the habitat patch sizes, although not based on the inverse density–area relationship.

Keywords Density–area relationship · Extinction threshold · Aphids · Parasitoid wasps · Habitat loss · Minimum viable population size · Patch size · Scaling

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Introduction

Habitat destruction and fragmentation is one of the major drivers of biodiversity loss due mainly to anthropogenic disturbance, e.g., the expansion and intensification of modern agriculture (Tilman et al. 2002; Henle et al. 2004; Zhao et al. 2010). Designing a robust and sensitive estimate of the minimum amount of suitable habitat, known as the MASH, that can sustain a viable population has become a priority in conservation (e.g., Bart 1995; Akcakaya et al. 1999; Brito and Grelle 2006; McCoy and Mushinsky 1999, 2007; Zhao et al. 2011). The existence of the MASH for species long-term persistence provides us a practical tool, by manipulating the patch size of focal species, to ensure the survival of endangered species and the successful control of the problematic ones (such as pests and invasive species; Brook et al. 2000; Engen and Sather 2000). Indeed, the MASH has been considered a critical indicator for assessing the conservation status of endangered species (Shaffer 1981). Different species had different values of MASH, which reflect their different habitat requirements and differences in body size, migration, trophic level, and habitat quality. In general, the higher trophic level, the larger MASH. MASH has important implications for integrated pest management, and MASH itself can be used as a pest control tool, especially in agricultural landscape design. As an important aspect of conservation biological control (CBC), the ultimate direction of MASH was the construction and design of agricultural structure in successive spatial–temporal scale, which enhanced activity and predation of natural enemies in agricultural landscape, and suppressed the pest population to the greatest extent.

The MASH can generally be estimated by three methods (or defined in three ways): (1) the minimum patch size to ensure a certain probability of presence in a presence–absence survey (Vance et al. 2003); (2) the minimum patch size to ensure a population will persist with a certain probability of long-term survival in the

population viability analysis (Wielgus 2002); (3) the minimum patch size to ensure a positive population density according to the density–area relationship (Bender et al. 1998; Smallwood 2001). The density–area relationship is a well-studied pattern in habitat fragmentation experiments, but shows a considerable variability in the literature (e.g., Bender et al. 1998; Pearman 1993; Connor et al. 2000; Debinski and Holt 2000; Matter 2000; Gaston and Matter 2002; Hokit and Branch 2003). A positive density–area relationship is often found for insects and birds (Bender et al. 1998; Connor et al. 2000), whereas a negative or non-significant relationship for mammals (Bowers and Matter 1997). The correlations between patch size and habitat quality, migration rates, predatory pressure and social interactions have been proposed as potential mechanisms of the density–area relationship (Root 1973; Risch 1981; Matter 1997; Bowers and Matter 1997). Using burrow density of the gopher tortoise (*Gopherus polyphemus* Daudin), McCoy and Mushinsky (2007) demonstrated two practical methods for estimating the MASH from the density–area relationship: by visual and local polynomial regression. Importantly, they reported an inverse density–area relationship when the patch size is relatively small, and suggested that this inverse density–area relationship is a direct result from habitat loss (so that species are forced to stay in the remaining habitat).

Here we use the data of wheat aphids and their parasitoids and hyperparasitoids collected from an experiment of conservation biological control to present (1) the density–area relationships at three trophic levels, and (2) unveil the effect of patch size on the coupled dynamics of populations as well as the rate of parasitism and hyperparasitism. Conservation biological control is the practice of enhancing natural enemy efficacy through modification of the environment or the pesticide practices (Jonsson et al. 2008; Khan et al. 2008), of which the manipulation of habitat has been considered an important control strategy (Landis et al. 2000). Designing an agricultural landscape with appropriate patch sizes that can surpass the pest density in the crop field through enhancing its natural enemies is appealing (Kruss 2003). We also demonstrate that McCoy and Mushinsky's (2007) inverse density–area relationship is only an artifact due to the systematic variation in this relationship, and thus argue that using the systematic variation in the density–area relationship to determine the MASH could be misleading. Our results highlight the scale sensitivity of host–parasitoid interactions.

Materials and methods

Study species and experimental design

We chose 72 sites of wheat fields (divided by plastic film), ranging from 1.98 to 3,237 m^2, on the Yinchuan Plateau in the northwest of China in 2009. All sites were planted with spring wheat and had a density of 400–500 plants per m^2 when sampled. The major insect pests in fields were wheat aphids *Macrosiphum avenae* (Fabricius) and *Schizaphis graminum* (Rondani). The parasitoid wasps *Aphidius avenae* (Haliday) and *A. gifuensis* (Ashmead) were endoparasitic and an important control agent of wheat aphids (Powell 1982). Early appearance of parasitoid wasps often leads to a high proportion of parasitized aphids, which helps to reduce the population growth rate of aphids (Sigsgaard 2002). However, some parasitoid wasps were parasitized by hyperparasitoid wasps *Pachyneuron aphidis* (Bouche) and *Alloxysta* sp. that could be detrimental to the biological control.

Each site was visited three times: on May 2, May 28, and June 10, representing infancy, outbreak and stable periods of aphids. During each visit, a total of 500 straws were collected per site, including the aphids for further laboratory analysis. The collected aphids were reared on leaves of spring wheat in cylindrical plastic jars, in which the radius of bottom and height were 35 and 80 mm, respectively. The collected mummies were examined twice per day. Aphids that died during the rearing were dissected to examine whether they were parasitized. All laboratory-reared and field-collected mummies were identified to species and stored individually in gelatin capsules until the emergence of adult parasitoids or hyperparasitoids. The gelatin capsules were kept in test tubes sealed with a damp cotton plug at 20°C, with 14 h light and 10 h darkness in a climate chamber. The gelatin capsules with mummies were examined twice daily for the emergence of adults for the first month, and once every 2 days in the following month. Mummies, from which a parasitoid or a hyperparasitoid had not emerged for 2 months, were dissected to examine the cause and were classified as either aestivating or dead. A total number of 6,979 parasitoids and hyperparasitoids were identified.

Data analysis

Here we present the density–area relationships for all six species from three trophic levels and estimated their MASH using the two methods presented by McCoy and Mushinsky (2007): visual and local polynomial regression (Lowess smoothing; STATISTICA 9.0, StatSoft, Inc.). Because the wheat fields were homogenous in quality, a null hypothesis should be that the density is constant and independent from the patch size. Moreover, the rate of parasitism (the proportion of aphids parasitized by the parasitoid wasps, parasitism = $N_{\text{parasitoid}}/N_{\text{aphids}}$) and the rate of hyperparasitism (the proportion of hyperparasitoid wasps found on the parasitoid wasps, hyperparasitism = $N_{\text{hyperparasitoid}}/N_{\text{parasitoid}}$) were calculated by combining the individuals from the same trophic level together (aphids, parasitoids, and hyperparasitoids).

Results

The population densities of aphids, parasitoids, and hyperparasitoids confirmed the existence of the

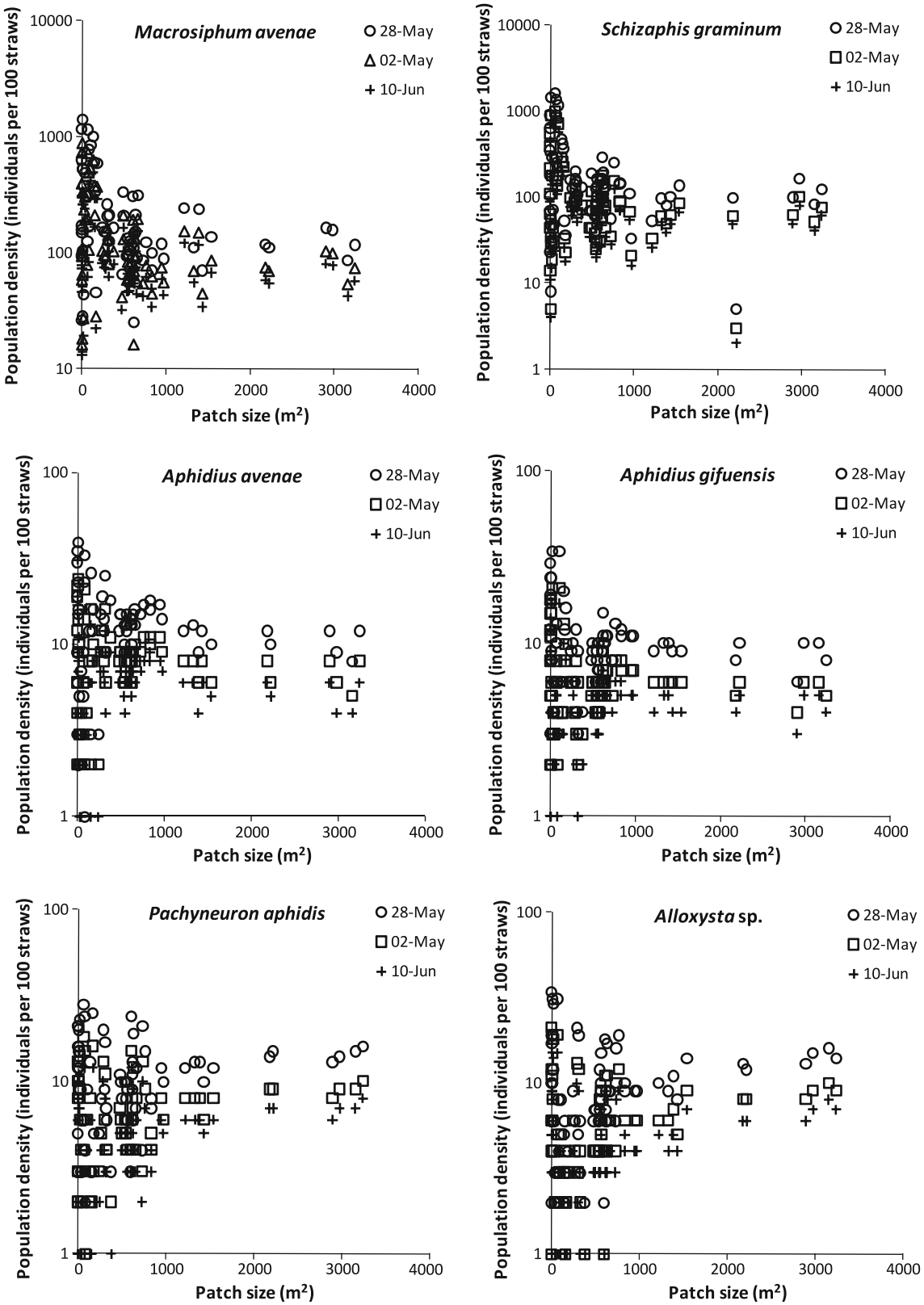

Fig. 1 Relationship between log-transformed population density and patch size of wheat aphids (*Macrosiphum avena* and *Schizaphis graminum*), parasitoids (*Aphidius avenae* and *A. gifuensis*) and hyperparasitoids (*Pachyneuron aphidis* and *Alloxysta* sp.)

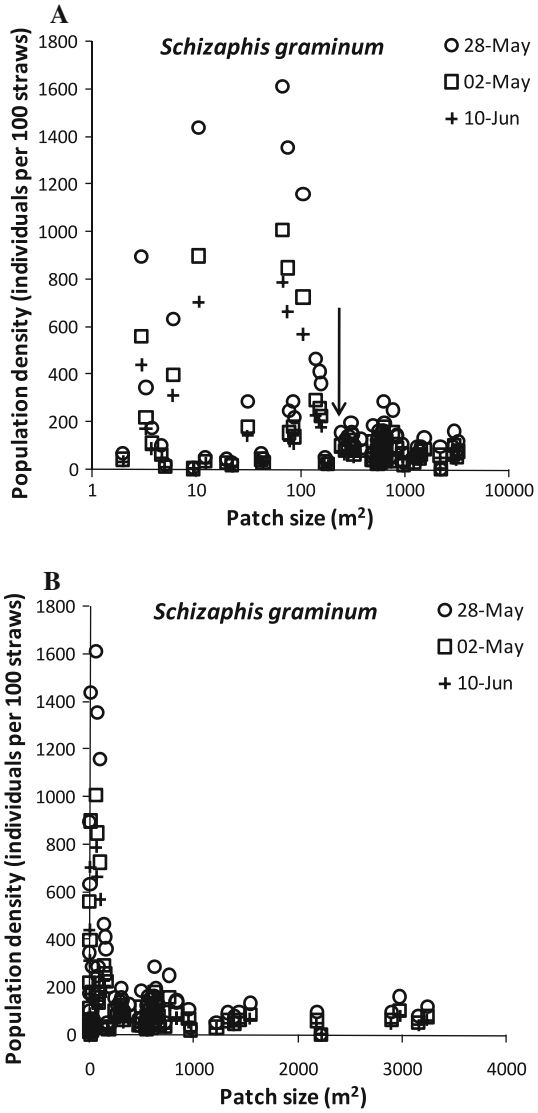

Fig. 2 Relationship between population density and patch size of the wheat aphid (*Schizaphis graminum*) when the patch size is log-transformed (**a**) and on the original antilog scales (**b**)

increasing variation of population density with decreasing patch size (Fig. 1). As the patch size larger, the population density became more stable (by comparing the data points from different sampling periods in Fig. 1). According to McCoy and Mushinsky's (2007) visual method, we estimated that the MASH for the aphid *M. avena* and *S. graminum* were both 246 m^2 [see an illustration for *S. graminum* in Fig. 2a, which was extremely similar to the Fig. 1 in McCoy and Mushinsky (2007)], the MASH for the parasitoid *A. avenae* and *A. gifuensis* were 479 and 495 m^2, and the MASH for the hyperparasitoid *P. aphidis* and *Alloxysta* sp. were 949 and 835 m^2, respectively. The inverse density–area relationship became more obvious after log-transformation than not log-transformation (Table 1). For example, it is evident that the inverse density–area relationship (Fig. 2a, b) is simply an artifact due to the log-transformation of patch sizes (Fig. 1), especially when the median of the populating density was low compared to the maximum population density. For instance, the median of *S. graminum* was 129.5 individuals per 100 straws (28 May), compared to its maximum population density of 1610 individuals per 100 straws, generating an illusion of a negative density–area relationship ($r = -0.30$, $p = 0.01$, Fig. 2a; $r = -0.25$, $p = 0.03$, Fig. 2b; Table 1), even though there was no correlation between the logarithmic density and patch sizes ($r = -0.19$, $p = 0.11$, Fig. 1; Table 1).

The local polynomial regression (Lowess smoothing) revealed a critical range of patch sizes for detecting the host–parasitoid relationship (Fig. 3). The patch size with the maximum aphid density was equal to the patch size with the minimum rate of parasitism (100 m^2, Fig. 3a, b). The patch size with the maximum rate of parasitism was nearly equal to the patch size with the minimum rate of hyperparasitism (500–1,000 m^2, Fig. 3b, c). To achieve maximum effect of biological control for reducing the aphid density by parasitoid wasps, the size of the wheat field should be greater than the MASH identified above for the parasitoid wasps (~500 m^2). Furthermore, there was a significant negative correlation

Table 1 Regression equations between population density and patch size of wheat aphids (*Macrosiphum avena* and *Schizaphis graminum*), parasitoids (*Aphidius avenae* and *A. gifuensis*) and hyperparasitoids (*Pachyneuron aphidis* and *Alloxysta* sp.)

Species		Regression equation	r	p
Macrosiphum avena	Not log-transformed	$Y = 112.51e^{-0.5265x}$	−0.38	0.04
	Log-transformed	$Y = 16.325e^{-0.1265x}$	−0.46	0.01
Schizaphis graminum	Not log-transformed	$Y = 153.62e^{-0.6512x}$	−0.30	0.01
	Log-transformed	$Y = 26.682e^{-0.2039x}$	−0.25	0.03
Aphidius avenae	Not log-transformed	$Y = 4.625e^{-0.165x}$	−0.48	0.03
	Log-transformed	$Y = 3.689e^{-0.1693x}$	−0.69	0.01
A. gifuensis	Not log-transformed	$Y = 6.3251e^{-0.2655x}$	−0.39	0.04
	Log-transformed	$Y = 3.9621e^{-0.1362x}$	−0.68	0.01
Pachyneuron aphidis	Not log-transformed	$Y = 28.3651e^{-0.2651x}$	−0.26	0.05
	Log-transformed	$Y = 5.965e^{-0.3629x}$	−0.42	0.02
Alloxysta sp.	Not log-transformed	$Y = 16.832e^{-0.2035x}$	−0.31	0.06
	Log-transformed	$Y = 4.9689e^{-0.1259x}$	−0.58	0.03

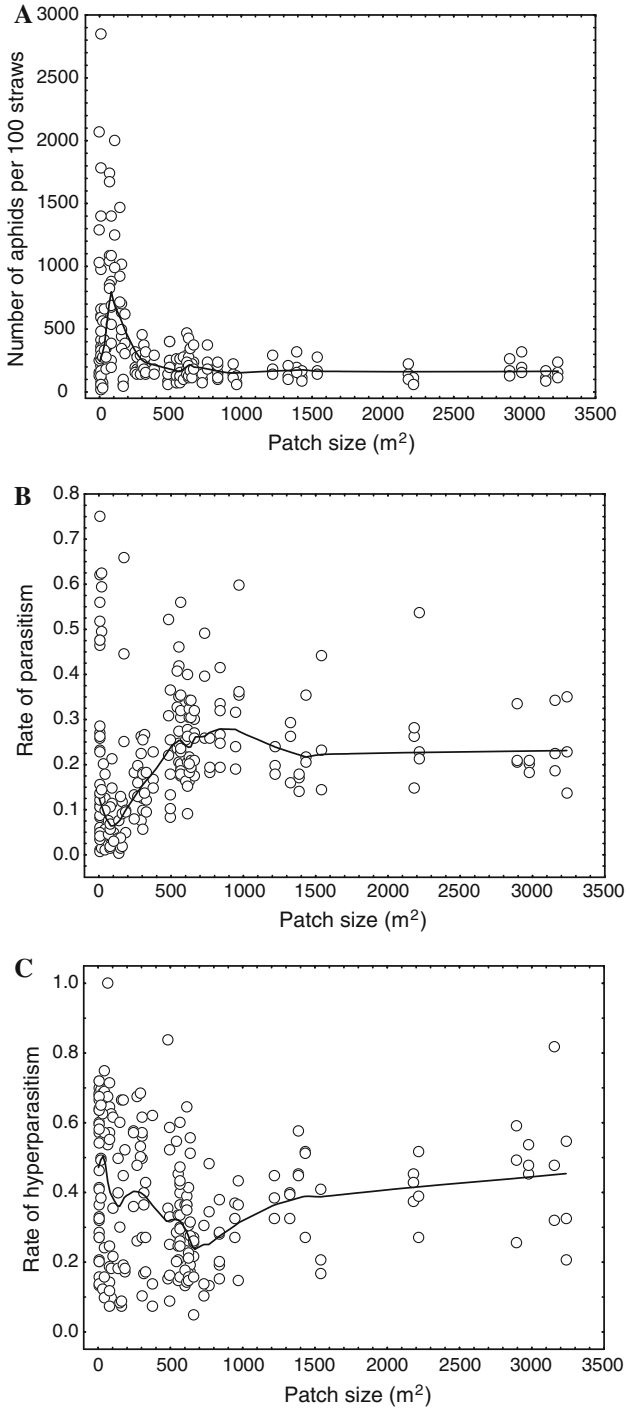

Fig. 3 Local polynomial regression of the effect of patch sizes on aphid population density (**a**), rate of parasitism (**b**), and rate of hyperparasitism (**c**)

and a power law relationship between the aphid density and the rate of parasitism ($r = -0.79$, $p < 0.01$, Fig. 4a). The negative correlation between the rate of parasitism and hyperparasitism was also significant ($r = -0.26$, $p < 0.01$) but the form was not as clear (Fig. 4b).

Discussion

An inverse (or negative) density–area relationship is not uncommon in the literature (Bender et al. 1998; Connor et al. 2000). This inverse density–area relationship could arise from the inclusion of large unoccupied habitat in large patches, the effect of plot shapes on migration rates, and sampling inefficiency in large patches (Gaston et al. 1999; Fahrig 2001; Gaston and Matter 2002). However, the inverse density–area relationship identified by McCoy and Mushinsky (2007) does not reflect a real negative correlation between the population density of gopher tortoises, rather it may be an artifact from the high spatial variation of population density on small patches (Fig. 2). Consequently, the MASH estimated from the two methods could be misleading if applied in conservation. As shown in the Fig. 1 of McCoy and Mushinsky (2007), the population densities on small patches remains high even after a decade, showing a lack of strong stochasticity (or fluctuation) of the gopher tortoises on small patches.

Our results also confirmed that the seasonal fluctuation of aphid population density was low, compared to the spatial variation of the population density (Fig. 1). As the habitat area became larger, the population density became more stable (Fig. 1). This defies the definition of the MASH though spatial variation. Designing smaller patches than the so-called MASH for biological control of the aphids can be problematic. To avoid generating an artificial inverse density–area relationship, the population density should be log-transformed (Figs. 1, 2).

The result that the host–parasitoid interactions work only at certain spatial scales (patch sizes) is not only consistent with the general conclusion from spatial ecology (Holling 1992), but also enables us to conduct successful biological control without encountering the environmental risk of pesticide. The application of this scale-dependence of host–parasitoid interaction, together with providing heterogeneous and refugee habitat for the natural enemies of pests, could beget efficient pest control in agricultural land (Sigsgaard 2002; With et al. 2002). The so-called MASH estimated from McCoy and Mushinsky's (2007) actually indicates the lower (or higher) bound of the interaction between the focal species and other species (or resources) on lower (or higher) trophic levels, i.e. the spatial scales at which the population regulation is most obvious. Specifically, we suggest a minimum patch size of 500 m^2 for efficient biological control of aphids, obviously not for sustaining them, in the spread wheat field (Fig. 3).

The discrepancy of the results on the density-dependent parasitism has long been noticed in literature. Although a positive correlation between host density and the rate of parasitism is an important stabilizer and promoter of the coexistence of the hosts and their parasitoids (Hassell and May 1973; Beddington et al. 1978), negative and no correlations are more widely observed empirically (Morrison and Strong 1980; Stiling 1987;

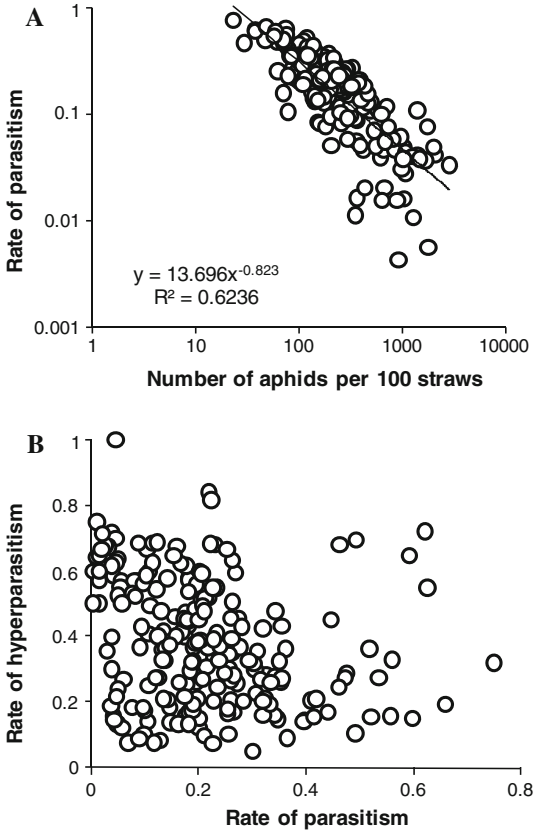

Fig. 4 Relationship between host density and the rate of parasitism (**a**). Relationship between the rate of parasitism and the rate of hyperparasitism (**b**)

Walde and Murdoch 1988) than positive density-dependent parasitism (Ives et al. 1993). Our result supports a negative density-dependent parasitism (Fig. 4). However, our data restrain us from further analyses of the potential mechanisms of this negative density-dependent parasitism, which could arise from (1) the prolonged handling time by the parasitoids when the host density is high (Hassell and May 1973), (2) the egg limitation in parasitoids (Morrison and Strong 1980), and (3) the risk reduction by scattering the eggs of parasitoids (Turchin and Kareiva 1989). Specifically, we identified a power law form of this density-dependent parasitism (Fig. 4a), which did not hold due to high variation at a higher trophic level (Fig. 4b). Overall, the scale-dependence and the systematic spatial variations of the host–parasitoid interaction suggests that we can achieve the optimal effect of biological control by manipulating the habitat patch sizes, although not based on the inverse density–area relationship.

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